Zootaxa 2946: 17–28 (2011)
www.mapress.com/zootaxa/

Editorial

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Numerical cladistics, an unintentional refuge for phenetics—a reply to Wiley et al.*

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**In*: Carvalho, M.R. de & Craig, M.T. (Eds) (2011) Morphological and Molecular Approaches to the Phylogeny of Fishes: Integration or Conflict?. *Zootaxa*, 2946, 1–142.

Abstract

The assertion that phylogenetic inference algorithms are not authoritarian because results are repeatable, predictable and freely available misses the point that the authority resides in underlying algorithm models that are not cladistic. We show that optimization procedures can group using symplesiomorphy and that optimization is not always equivalent to cladistic argumentation. Because parsimony and Bayesian algorithms can obtain the same answer from the same data set is not evidence that they are Hennigian; examples exist where these methods do not provide the same result from the same data. Using 'reversals' as evidence in systematics is problematic because the question, "Reversal to what?" has no straightforward answer. This confusion can be eliminated by recognizing that homologues are the parts of organisms and homologies are the relationships between the parts, and that the latter is a hierarchical concept rather than transformational. We clarify that Hennig's auxiliary principle pertains to *potential* synapomorphy, meaning for molecular work that it is the presence of a particular *derived* nucleotide that is shared in a given position of aligned sequences of two or more taxa that should be considered homologous until proven otherwise, not simply the alignments themselves. We reiterate that not all data are evidence and we specifically reject homoplasy as a source of 'evidence' for systematics. We further reject the view that conflict among data should be resolved through methodology. It is the data that should be our primary focus, as it is our attempts to identify and clarify homologues worthy of suggesting relationships (homology) that are primary in systematics.

Introduction

Recently, two of us wrote a paper addressing what we perceived to be a crisis in systematic ichthyology (Mooi & Gill 2010a). It has subsequently received some attention, including an evaluation from Wiley et al. (2011). They felt that Mooi & Gill's arguments could be reduced to four basic claims, all of which they argued were either false or irrelevant:

1 The reliance on optimization algorithms is the modern incarnation of authority-based taxonomy;
2 Outgroup comparisons no longer play a critical role in determining character polarity;
3 The use of optimizations to build trees is not cladistic;
4 Not showing synapomorphies on a phylogeny obscures the readers' ability to judge alternative hypotheses, and measures of node support (and other statistical manipulations) do not refer to the quality of individual characters and their states.

Here we address the criticisms of those four claims and in so doing, expand on and restate a few related issues. Wiley et al.'s response is largely based on issues concerning the claim headings, but additional (and often tangential) matters are also discussed under the same headings. In addition, some issues are discussed across several head-

Accepted by M.R. de Carvalho: 2 May 2011; published: 8 Jul. 2011

ings. In order that our response may be more coherent to readers, we have organized them under new headings that more accurately address the key issues. Commentary in Wiley et al. concerning either Mooi and Gill's credibility as systematists or assumed hidden agenda are distractions from the intended message of the original paper and also from this counter response. We therefore respond to these points separately (Gill & Mooi 2011).

Algorithms as Authorities

Wiley et al. (2011:8) contend that Mooi and Gill (2010a) were wrong to equate modern methods that find trees under various optimality criteria with "authority," because the results of these methods are repeatable, predictable, and available to anyone:

> "If one does not agree with the limits and relationships of Thacker's (2009) gobiiforms, Smith and Craig's (2007) perciforms, or Miya et al.'s (2007) lampriforms, one can easily obtain these data and reanalyze them, or gather new data (molecular or morphological) and combine them with the original data."

The point of the original comment was that the authority resides in the algorithms and their in-built assumptions (models, if you will). This was the basis of Mooi & Gill's complaint about optimization: if the assumptions are erroneous, then, no matter how repeatable the results, they too will be wrong. That is the nature of authority.

Outgroup Comparisons

Wiley et al. (2011: 10) provide a list of recent papers that incorporate outgroups and proclaim:

> "…the charge that outgroups are disregarded by phylogeneticists using molecular data is simply untrue as a matter of published record."

Mooi & Gill (2010a) were, of course, not referring to phylogeneticists not incorporating outgroups, but to the methods themselves. The inclusion of taxa outside the group of interest is no guarantee that they are being used effectively as outgroups. The majority of studies use a single (often very distantly related) species to root the optimized network and initiate tree structure, in effect using that single species as the outgroup rather than information held in the multiple outgroups implied by the taxon sampling. Choice of outgroup is made moot by optimization methods in any event, as all variation (apomorphic, symplesiomorphic and homoplastic) is employed to construct trees.

Methodology and Phenetics

Wiley et al. (2011: 11) contend that

> "…there are four methods of phylogenetic analyses that do not rely on phenetic (distance estimates) methodology: (1) classical Hennigian argumentation, (2) parsimony analysis, (3) likelihood analysis, and (4) Bayesian inference. Of the four, Hennig is known to us only to have used Hennigian argumentation."

Wiley et al.'s view that phenetic methodology pertains only to "distance estimates" is too narrow a view, though perhaps a commonly misunderstood one. We, instead, view phenetic methods as any method that estimates relationships by overall similarity:

> "…we may redefine *phenetic relationship as similarity (resemblance) based on a set of phenotypic characteristics of the objects or organisms under study.* [...] Phenetics is that aspect of taxonomic relationship concerned with phenetic relationships but it is also used as synonymous with the study of phenetic relationships" (Sneath & Sokal 1973: 29, original italics).

Therefore, our view that many current optimization methods are phenetic is in keeping with their use of including both synapomorphy and symplesiomorphy for determining relationships. A concern is that optimization methods may group by symplesiomorphy, a matter that is not simply imagined.

Optimization and Argumentation: Are They the Same?

Wiley et al. (2011: 11) offered the following on the connection between parsimony and Hennigian argumentation:

> "At least one of us (EOW) is old enough to have also used classical Hennigian argumentation in publication (Wiley, 1976) and can speak directly to why he began using parsimony algorithms as an alternative: Parsimony algorithms mimic classical Hennigian argumentation. They are simply more efficient, especially in the face of conflicting data."

Does parsimony mimic classical Hennigian argumentation, or is this merely assertion?

Consider the simplest matrix possible, with one character and four taxa, A—D (plus an outgroup):

OUT	0
A	0
B	0
C	1
D	1

Parsimony analysis of that matrix yields one solution: AB(CD). We expect no disagreement as there is no conflicting evidence. Consider a slightly more complex matrix, with two characters and four taxa, A—D (plus an outgroup):

OUT	0	0
A	0	0
B	0	1
C	1	0
D	1	1

This presents some conflict as the first character implies the relationship AB(CD), the second AC(BD). Parsimony analysis of that matrix yields four solutions:

A(C(BD))	AC(BD)
A(B(CD))	AB(CD)

The first column has two fully resolved solutions, the second repeats the two original characters, the overall summary (the strict consensus) is ABCD: no solution. One might intuitively understand the solution to be A(BCD).

Consider a further more complex matrix, with three characters and four taxa, A—D (plus an outgroup):

OUT	0	0	0
A	0	0	0
B	0	1	1
C	1	0	1
D	1	1	0

This presents more conflict as the first character implies the relationship AB(CD), the second AC(BD), the third AD(BC). As with the two character matrix above, one might intuitively believe the solution to be A(BCD). Parsimony analysis yields six solutions:

A(D(BC))	AD(BC)
A(C(BD))	AC(BD)
A(B(CD))	AB(CD)

The first column has three fully resolved solutions, the second repeats the three original characters[1]. The overall summary (the strict consensus) is ABCD: no solution, the bush. One might imagine that for this matrix too the intuitive solution, A(BCD), is better, or more exact, than the analyzed solution. Taxon A has all plesiomorphic values and these data clearly do not speak directly to its relationships with B, C or D, yet there is evidence for BC, CD and BD being more closely related to each other than they are to A.

Nelson (1996) explored 120 matrices of this kind. One conclusion was that in matrices with all conflicting characters "a group is resolved in 96 of 120 cases – enough to suggest that evidence of a group is a general property of matrices of this kind. In 24 cases, however, the strict consensus is uninformative. If evidence of a group is present in each matrix, then the program fails to find the evidence in 20% of the cases." By a group, it is meant that all taxa are more closely related to each than they are to A, such as A(BCD) for the three character matrix above. That is, optimization handles data idiosyncratically. We conclude, therefore, that optimization is the source of the problem.

Consider a second example, from Goloboff et al. (2003), with a matrix that yields one tree B(C(D(E(F(GH))))) [where A is the outgroup]. The matrix is:

	1	2	3	4	5
A	0	0	0	0	0
B	1	0	0	0	0
C	1	0	0	0	1
D	1	0	0	1	1
E	0	0	0	1	1
F	0	0	1	1	1
G	0	1	1	1	1
H	1	1	1	1	1

If character 1 is omitted the most parsimonious tree is B(C(DE(F(GH)))). Character 1 offers the following evidence: EFG(BCDH). With parsimony, the combination of these two results yields B(C(D(E(F(GH))))), 'creating' the node D(EFGH). Inspection of the matrix reveals no direct evidence for D(EFGH). Goloboff remarks: "The only character that provides a synapomorphy for the EFGH branch is character 1. Character 1 by itself does not provide support for EFGH, since eliminating any of the other characters (which seem otherwise irrelevant to the monophyly of EFGH) also eliminates EFGH. The only character that contradicts EFGH is character 1, the same character that appears as its synapomorphy" (Goloboff et al. 2003: 326). Once again, we are forced to conclude that optimization is the source of the problem, rather than appropriate support.

Finally, consider a third example from data first offered by Goloboff and Pol (2002; discussed further in Williams 2007 and Williams & Ebach, 2010):

1. The analyses were performed using Hennig86 (Farris 1988). With NONA (Goloboff 1993) only two and three trees are recovered, respectively. NONA does not yield the two-node fully resolved trees.

	1	2	3	4	5	6	7	8
Root	0	0	0	0	0	0	0	0
A	0	0	0	0	1	1	1	0
B	1	0	0	0	1	1	1	1
C	1	1	1	0	0	0	0	0
D	1	1	1	0	1	0	0	0
E	1	1	1	1	1	1	0	0
F	1	1	1	1	1	1	1	1

Parsimony analysis yields four equally parsimonious trees:

C(D((AB)(EF)))
C((AB)(D(EF)))
(AB)(C(D(EF)))
C(D(E(F(AB))))

Each tree differs with the exception of the AB node; this suggests an appropriate summary of the data is (AB)CDEF, the result obtained from strict consensus. As an aside, two non-cladistic analyses – UPGMA and neighbour-joining (NJ) – also retrieved the same AB node, though differing in other details (retrieving the trees C(AB)(F(DE)) and C(AB)(D(EF)), respectively). Because the AB node re-occurs, it seems reasonable to consider it a real result (that is, a natural grouping), the only such result for the data matrix. However, inspection of the matrix reveals that A and B share only 0 entries, that is the relationship is entirely supported by symplesiomorphy. Such relationships are explained away by the vague notion of "character reversal." But what exactly does this mean? We deal with that later. Yet again, we are forced to conclude that optimization is the source of the problem. It is not Hennig or his proposals concerning argumentation plans (where relationships are investigated only on the basis of *a priori* hypotheses of synapomorphy) but its supposed equivalence to Wagner parsimony.

The claim made by Wiley et al. that parsimony algorithms mimic classical Hennigian argumentation contrasts to one made during the early development of parsimony algorithms:

> "The most significant difference between the two approaches concerns the fact that Phylogenetic Systematics [Hennigian argumentation] estimates only the cladistic parameter and in doing so it uses only derived states. Quantitative Phyletics [as applied in parsimony algorithms] estimates both cladistics and patristics and it uses all states, derived and primitive, in those estimations . . . to ignore similarity based on shared primitive states can lead to significantly different phylogenetic hypotheses" (Kluge 1976: 43).

Indeed it can – how many of those "significantly different phylogenetic hypotheses" are the products of the "blender of optimization" (Mooi & Gill 2010a)?

Wiley et al. present two examples designed to show the equivalence of parsimony analyses and Bayesian analyses. In effect, their claim is that Bayesian analyses are Hennigian inasmuch as they group by synapomorphy, a claim no one has ever made before. Leaving aside our differences over the meaning of synapomorphy, homologues and homology, Wiley et al. illustrated this claim first with an analysis of data derived from Gauthier et al. (1988), who present a matrix of characters relating to amniote relationships (fossil and Recent). Their parsimony analysis yielded one tree. The same tree was found by their Bayesian analysis. There were 198 unambiguous synapomorphies that supported the tree, the same that appeared on the Bayesian tree. Their second example, drawn from fishes, makes essentially the same point. They concluded:

> "…these demonstrations reveal that sweeping generalizations that statistical approaches to phylogeny reconstruction are not based on synapomorphies are simply untrue. The Bayesian analyses resulted in monophyletic groups confirmed by synapomorphies, and the placement of these synapomorphies in the case of the amniote analysis was identical to the placement of synapomorphies in a parsimony context and, we would assume, a traditional Hennigian argumentation analysis" (Wiley et al. 2011: 13)

First, with the amniote example, as it's the same tree one would expect the nodes to be supported by the same synapomorphies—that is a property of the data not the method. Second, one need only glance at recent issues of *Molecular Phylogenetics and Evolution*, for example, and find literally hundreds of papers with conflicting results derived from parsimony and Bayesian analyses, respectively. We find their conclusion—that parsimony = Bayesian = Hennig—utterly bizarre.

On Zeroes: Transformational Homology, Symplesiomorphy and Reversals

Wiley et al. (2011: 8) commented that

> "Their [Mooi and Gill] treatment of homology, however, is curious. Mooi and Gill state that within a transformation series the states coded "one" are apomorphic but the states coded "zero" are not equivalent among taxa. This, they state, is because the code "zero" (0) only means "not having one" (1). But is this true? Consider a column of data where the presence of pectoral fins is coded "zero" and the presence of forelimbs is coded "one." Do all taxa coded with "zeros" share a state? Of course they do, and, in fact, this state is homologous among all taxa with pectoral fins. Are pectoral fins homologous with forelimbs? Yes, given present knowledge. They are, in the sense of Wiley (2008), "transformational homologues," in that one is a property of a larger monophyletic group (Gnathostomata) that includes a smaller monophyletic group within it (Tetrapoda) that has the apomorphic property. (Naturally we would have to include a lamprey to formally polarize the transformation series). So the sweeping generalization that "…having a 0 only means 'not having 1' – which means: we have no further information" (M&G, pg. 30) seems, at best, misplaced, and, at worst, a misunderstanding of homology itself. The whole point of the distinction between plesiomorphy and apomorphy is that one character (the plesiomorphy), homologous among basal members of a monophyletic group, is changed into another character (the apomorphy) in an ancestor of a less inclusive monophyletic group. Without plesiomorphic homologues, there can be no apomorphic homologues."

This is an important issue because (among other things) it is relevant to the above-mentioned concept of character reversal in optimization methods. If 0s do not imply a unified grouping, then the concept of "reversal" becomes problematic. However, we believe that Wiley et al. are incorrect in their conclusion, and that this is a result of confusing the terms "homologue" and "homology," and that this confusion extends into molecular systematics. For us, the distinction between these terms was clarified by Nelson (1994): homologues are the parts of organisms (prepectoral fins, pectoral fins and forelimbs in Wiley et al.'s example), and homologies are the relationships between the parts (e.g., forelimbs in Wiley et al.'s example suggest that tetrapods are more closely related to each other than to other vertebrates). As noted by Nelson, this distinction is in keeping with Owen's original definitions.

To expand on this, Wiley et al. would have it that the 0s (that is the non-forelimb pectoral fins) of a lungfish, a flying gurnard, a flying fish, a shark, and ray imply a relationship. But we have good evidence that this is not the case; for example, the pectoral fins of a lungfish are more closely related to the forelimbs of a tetrapod (e.g., Gill 1872). Of course, one could introduce more character states in an attempt to counter this, but as it stands, taxa with 0 do not indicate a relationship: the 0s indicate symplesiomorphy. Only the 1's (tetrapod limbs) indicate a relationship, that tetrapod limbs are more closely related to each other than to any of the "unmodified" pectoral fins. The confusion results from imposing an ancestral-descendant notion on homologues, in other words, character transformation. As Nelson (1994) put it (p. 127): "Characters seen as part of the same transformation series were claimed by early cladists to be homologous, and it is now evident that the claim is defective, for it construes the transformation series as "fin"-"arms"-"wings" [or in Wiley et al.'s case, "prepectoral fins"-"pectoral fins"-"tetrapod limbs"], that is as including symplesiomorphy." Nelson went on to say (p.127) "It is curious, but not surprising in retrospect, that cladists abandoned the traditional notion of relationship of taxa (one group of organisms ancestral to another) but retained the same notion for relationship of characters (one group or characters ancestral to another) – as if whole organisms were related in a way different from their parts. Cladists routinely reject statements such as birds evolved from reptiles [or in Wiley et al.'s case, tetrapods evolved from fish], and accept statements such as bird wings evolved from arms [or forelimbs from pectoral fins], when the two sorts of statements, to the extent that they

mean anything at all, mean exactly the same thing: such as, the relationship among birds [or tetrapods] (and some of their parts) is one and the same node of life's hierarchy."

Nelson (1994: 137) later concludes: "A cladogram differs from other types of phylogenetic trees in placing all organisms, both fossil and present, in terminal positions, implying that ancestral taxa are artifacts. Cladistics may possibly be improved if parts of organisms were treated in the same fashion in character (state) trees, with the implication that ancestral characters, too, are artifacts."

So what then is a "character reversal"? Optimizers would have it that it is a return to the 0 state from the 1 state (see examples above). But, in the case of Wiley et al.'s example, which version of 0 would this be, the pectoral fin of a lungfish, a flying gurnard, a flying fish, a shark, a ray, all of them, or some subset? It is perhaps unfair to call this phenetic reasoning, as it is doubtful that any pheneticist would actually equate all of these morphologies. As Platnick et al. (1996: 248) summed up: "After all, grouping A and B together simply because they lack a feature that unites C and D was recognized as barbaric centuries ago, by Plato. One wonders how long it will take for systematists to realize that allowing the "0" entries for taxa A and B to constrain potential resolutions can also give this sort of "negative evidence" more weight than it deserves…".

Transformational Homology versus Hierarchical Relationship

The problem of transformational homology (as used by Wiley (2008) and Wiley et al. (2011)), may be further explored and contrasted with hierarchical relationship, two issues that are confused by Wiley et al. Transformational homology implies certain things about the two compared characters. Consider Wiley et al.'s (2011:8) statement:

> "The whole point of the distinction between plesiomorphy and apomorphy is that one character (the plesiomorphy), homologous among basal members of a monophyletic group, is changed into another character (the apomorphy) in an ancestor of a less inclusive monophyletic group."

In this case the assumption is:

A	B		C	D
0	0	→	1	1

This notation is read as 0 'turns into' 1. But, from the perspective of transformation, when 0 transforms to 1 does it then disappear, become completely 1, so to speak? No, as transformation means just that: transforming. So the notation would be better represented as:

A	B	C	D
0	0	0	0
		1	1

That is a hierarchical relationship, 00(11), such "that one is a property of a larger monophyletic group (Gnathostomata) that includes a smaller monophyletic group within it (Tetrapoda) that has the apomorphic property" (Wiley et al. 2011: 8). Thus Gnathostomata stand in hierarchical relationship to Tetrapoda, just as 0 stands in hierarchical relationship to 1.

One might imagine that 0 → 1 is the same as 00(11) and any efforts to claims that the ""zero" should mean something" seem misplaced and appeals to evolution simply wrong-headed ("If it does not, then where is the evolution?"). However, for the zero to mean something, the assumption must be that instead of 00(11) we have (00)(11), a phenetic representation of data, devoid of any sense of relationship. Such a phenetic representation allows the coded values to float around the various optimal trees so that something being homoplasious could also be synapomorphic: "Further, if the distribution of thymine on a tree does indicate homoplasy, then it is possible that two or more subclades have the synapomorphic property 'thymine present.' What is homoplastic at one level (the entire transformation series) may be locally synapomorphic (i.e, homoplasy at one level may be homology at

another; otherwise, synapomorphies would always have a consistency index of 1)" (Wiley et al. 2011: 9). Thus, it would seem, "grouping by homoplasy" is being advocated, albeit disguised within the parameters of a particular algorithm. To claim that this is achieved through congruence – "pitting one hypothesis of synapomorphy against another in the arena of what is now called 'optimization'" – simply mangles homology and synapomorphy as they become byproducts of an algorithm.

Homoplasy

Homoplasy was a term created by Lankester (1870) to account for what he saw as 'similarities' that could not be explained by direct common ancestry. Källersjö et al. (1999) stated clearly what others had actually been doing and it became a further (molecular) justification for the notion that 'amounts' of similarity could count as synapomorphy ("…rapidly evolving and highly homoplastic, third positions contain most of the phylogenetic structure in the data" Källersjö et al. 1999: 91, abstract – actually the title of their paper explains this quite clearly). The general argument is this. If you can maximize as much of the 'similarity' as possible as synapomorphy (evidence of a group) then this was advantageous. Consider this single character:

A	0
B	0
C	1
D	0
E	1
F	0
G	1
H	0
I	1

For us, the clear synapomorphy (evidence of a group) is ABDFH(CEGI). But if free reign is given to the overall congruence of characters, CEG, CEI, EGI, CE, CG, CI, EG, EI, and GI could all contribute to group definition (evidence of a group). That is, if other data found the group CEG, then the above character would provide support for it. Imagine, then, if the 0s are given this same attention. This allows another suite of potential groups (ABDFH, ABDF, ABDH, etc.), until there is an endless array of relationships derived from the study of one homologue, "witnessing the re-emergence, even vindication, of phenetics as the "overall similarity of synapomorphy" (Nelson 2004: 139).

Hennig's Auxiliary Principle

Wiley et al. (2011: 9) contend that,

> "Mooi and Gill make another curious statement when they refer to alternate character states in a DNA matrix. They claim that the alternate states at an aligned position are not homologous with the derived state. In this, they completely misunderstand molecular homology where base pairs at a particular position in the gene, as shown by the alignment, are considered homologous until proven otherwise (following Hennig's Auxilliary [sic] Criterion; Hennig, 1966)."

So, what exactly is Hennig's auxiliary principle? Hennig (1966: 121) said:

> "I have therefore called it an "auxiliary principle" that the presence of apomorphous characters in different species is always reason for suspecting kinship [i.e., that the species belong to a monophyletic group], and that their origin by convergence should not be assumed a priori (Hennig 1953)."

In other words Hennig's auxiliary principle pertains to *potential* synapomorphy – thus the presence of a particular *derived* nucleotide that is shared in a given position of aligned sequences of two or more taxa, not simply the alignments themselves, as advocated by Wiley et al. Moreover, Hennig was even more explicit with regard to this:

> "Metabolic types" (as well as other "chemical characters" of the species) can be used for disclosing phylogenetic relationships only if series of transformations - similar to those among the morphological characters - can be recognised among them, and if the plesiomorphous conditions can be distinguished from apomorphous conditions in these series" (Hennig 1966: 102).

In short, regardless of the type of character, Hennig was explicit in demanding that only putative (*a priori*) synapomorphies are appropriate for phylogenetic analysis.

Dealing with Conflict

Wiley et al. (2011) repeatedly contend that Mooi and Gill (2010a) argued for use only of characters that are "understood" and that we advocated by-hand analysis only. This is simply not true. The point instead was that careful evaluation of each character was needed in order that putative apomorphic characters are correctly identified prior to analysis. This should be done through reference to available background information, such as ontogeny and outgroup comparison. This is what was meant (though perhaps vaguely stated) by "use biology not algorithms" to evaluate characters. Morrison (2009: 155) appears to agree that this is required for molecular characters as well:

> "There is an oft-repeated claim that sequences are easier to deal with than phenotypic characters because DNA sequences consist of only 4 types of nucleotides. However, it is straightforward to see that this fact makes homology assessment harder, not easier…We need to find the molecular equivalent of the well-known criteria for primary homology of phenotypic characters, such as topological correspondence, special similarity, intermediate forms, ontogeny, etc (Rieppel and Kearney 2002)."

Furthermore, although alternative analytical methods were not mentioned by Mooi and Gill, at no stage did we say that analyses could not be computer assisted. We are well aware of character conflict (see above). Our concern is that prevailing methods (such as parsimony, maximum likelihood and Bayesian analyses) suffer from the problems outlined above: in particular, no distinction is made between apomorphic and plesiomorphic characters, allowing taxa to be potentially grouped by symplesiomorphy and other distortions.

We suggest 3-item analysis (3ia) as an alternative, because it evaluates characters appropriately: 0 entries are correctly considered to be missing observations (= "not 1") rather than the basis for possible relationship. In so doing, we further acknowledge that the objectives of systematic investigation rest essentially with the testing of competing homology hypotheses by addressing the following questions: What are the hypothetical relationships (in terms of 3-item statements, the cladistic parameter) implied by a given putative synapomorphy? Which of these relationships is consistent with those of other putative synapomorphies?

The Usefulness of Support Measures

Wiley et al. (2011: 12) summarize a fourth claim thus: "Not showing synapomorphies on a phylogeny obscures the readers' ability to judge alternative hypotheses, and measures of node support do not refer to the quality of individual characters and their states. Instead these supports refer to more abstract measures, such as bootstrap support or conditional probabilities." We refer the reader to our second example above, in the "Optimization and Argumentation: Are They the Same?" section. That matrix was designed to illustrate the need for support measures, as character 1 is clearly behaving in an odd way. Goloboff et al. (2003: 326) explain it thus: "The example …shows that, for a given group, it may not be possible to divide the characters into those that are favorable, contradictory, or irrelevant: character 1 would fit two categories at the same time." But we see the situation differently. As we stated above, we see character 1 as providing evidence for the EFG(BCDH) relationship. Our studies revealed homologues relevant to the claim: that the homology statement is EFG(BCDH). Mathematical claims about its relevance are simply beside the point.

We need to stress here that this response, and the earlier commentaries (Mooi & Gill 2010ab; Williams 2007; Williams & Ebach 2010), are not attempts to destroy molecular studies or to subvert molecular systematics. In fact, it is the very opposite. We would like to see such data treated with the same respect that morphological characters have been, as individually meaningful, not merely part of some numerical 'averaging' or, perhaps, smearing. Once again it relates to how characters (data) are viewed such that it is '... not so much how best to analyze a data matrix, but how best to represent organismic variation in the matrix' (Platnick 1989: 21).

Increased Objectivity

Wiley et al. (2011: 8) state:

> "If one wishes to view the synapomorphies supporting particular nodes, one need only to download the data from Genbank and perform ancestral states reconstruction for all the characters in the analyses. The availability of these characters from nearly every molecular phylogeny is a vast improvement over previous phylogenetic studies where raw data used to generate phylogenies were not available and only interpreted data were available in matrices (when published) or character descriptions/illustrations in the body of the paper."

Their claim is that molecular data are more objective. Such a claim ignores assumptions used when aligning sequences prior to (or, in the case of "dynamic homology" as used by Smith & Wheeler 2004 and Smith & Craig 2007, during) phylogenetic analyses. It is, for instance, revealing to search recent molecular literature for the phrase "sequences were aligned by eye". Manual alignment without explicit criteria continues to be common place, particularly in adjusting algorithm-aided alignment (which in turn may also differ depending on the alignment algorithms used) (Morrison 2009). Alignment differences aside, one may also question whether it is appropriate to simply map characters on to solutions (trees) and claim that this procedure somehow identifies evidence (synapomorphies).

It is true, sequences can be downloaded directly from Genbank. It is also true that specimens can be requested from museums or other such institutes.

Homologue vs Homology

We noted above that the distinction between homologue and homology was clarified by Nelson (1994, 2011): homologues are the parts of organisms, homologies are the relationships between the parts. Thus, biological studies are focused towards homologues and their determination: homology is not simply 11 but 0(11), a hierarchical concept. It appears to us that molecular systematics rests with just the homologues and makes no specific hypotheses of homology – these are determined by whatever kind of optimization algorithm is applied, hence our earlier argument for biological over algorithmic homology. Thus, each 'new' molecular phylogeny produced for any given set of taxa is not built on any previous 'hypotheses' but become separate and unrelated. There is no progress in understanding – only a different and ever-changing picture of relationships that is tied to the ingenuity of the mathematics. Wiley et al. (2011: 13) noted that "…these demonstrations reveal that sweeping generalizations that statistical approaches to phylogeny reconstruction are not based on synapomorphies are simply untrue." Yet it doesn't appear that way to us.

Discussion

Wiley et al. (2011: 14) suggest, "The more conflict in the data, the more tools we need to employ to sort out the mess. Different methods have different advantages." The view appears to be that to resolve conflict we should turn to methodology. Our central message above is that it is the data that should have our primary interest, our attempts to identify and clarify homologues worthy of suggesting relationships. Although discussed in a slightly different

context, the reference to total evidence versus relevant evidence by Naylor and Adams (2003) is worth considering; we might reword the issue as total data versus relevant homologues. The desire should be to screen characters for usefulness, rather than combine all variation together in one big holy mess. These kinds of data are simply assembled to get a result rather than interpreting characters and identifying evidence. This is, indeed, moving ever nearer to Nelson's "stuff of nightmares" (2004: 139). Wiley et al. (2011: 14) note: "In the end, we are left wondering what M&G will argue against as we progress into whole-genome phylogenetic analyses…" We argue against the nightmare:

> "…the matrix of total evidence tends toward the biggest, the matrix with no real homologies at all, with all its characters homoplastic, when all of them change by optimization on the best fitting tree of an inexact solution…with each succeeding best fit determined by shifting pyramids of homoplastic characters, first distorted one way, then another" (Nelson 2004: 139)

Is this how systematics ends? Or is it possible that the community can recognize a Crisis in Systematics and take some remedial action?

Acknowledgements

We thank M.R. de Carvalho and M.T. Craig for organizing this special issue of *Zootaxa* and for the opportunity to reiterate and clarify our positions on what are critical issues for systematics. We also appreciate discussions with M. Ebach, G. Nelson and Willy Hennig on these issues. This paper is based on research supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant 327844-06 (RDM) and a Natural Science Foundation (USA) award DEB-0541914 (ACG).

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